A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 100: 1–22 (2025)
DOI: 10.3897/neobiota.100.143555

Research Article

Prepare for trouble and make it double: Effects of *Carpobrotus acinaciformis* and *Apis mellifera* invasion in floral visitor networks

Luiz F. C. Serigheli[1], Sofia Bacca[2], Brisa Marciniak[1], Michele S. Dechoum[1]

1 *Ecology of Biological Invasions, Management and Conservation Lab - Department of Ecology and Zoology, Universidade Federal de Santa Catarina, Florianópolis, 88010-970, Santa Catarina, Brazil*

2 *Biological Sciences Undergraduate student, Center of Biological Sciences, Universidade Federal de Santa Catarina, Florianópolis, 88010-970, Santa Catarina, Brazil*

Corresponding author: Luiz F. C. Serigheli (luiz_serigheli@hotmail.com)

Abstract

Invasive species pose a significant threat to ecological systems, impacting biodiversity and ecosystem functioning. Invasive plants and bees can alter mutualistic networks by increasing nestedness and reducing modularity, as a consequence leading to a reduction in network biodiversity and specialization. In this study, we investigated the ecological consequences of invasion by the non-native plant *Carpobrotus acinaciformis* and the non-native bee *Apis mellifera*, as well as the effects of controlling the invasive plant species on bee-plant interaction networks in coastal ecosystems. Our hypothesis is that *C. acinaciformis*, a melitophilous invasive plant, and *A. mellifera*, a generalist forager, both influence interaction networks, and that their control can alter network structure. Fieldwork was carried out in the Dunas da Lagoa da Conceição Natural Municipal Park, in southern Brazil, with active searches and collection of bees and flowering plants in areas invaded and uninvaded by *C. acinaciformis* in year 1 of the study. Collection procedures were repeated in uninvaded and managed areas after *C. acinaciformis* was subjected to mechanical control in year 2. We compared interaction network metrics between invaded and uninvaded areas in year 1 and between managed and uninvaded areas in year 2 using null models. We also simulated the elimination of *A. mellifera* from all networks (invaded, uninvaded, and managed) as a first step to understanding the effects of invasive honey bees. This simulation suggests that *A. mellifera* invasion increases nestedness and reduces modularity of the interaction networks. The elimination of the invasive plant and the simulated removal of the invasive bee led to changes in network dynamics, suggesting potential shifts that increased the stability and specialization of interaction networks. Our findings contribute to the understanding of the intrinsic interactions between invasive species such as *C. acinaciformis* and *A. mellifera* and native bee-plant networks. We emphasize the need for long-term studies using multiple methodologies, including field experiments and simulations, to generate comprehensive assessments for building knowledge on biological invasions and management. This enables adaptive and effective management strategies to mitigate the impacts of invasive species on ecosystem dynamics and biodiversity conservation.

Key words: Bee-plant interaction, ecological networks, invasive species, management

OPEN ACCESS

Academic editor: Ruth Hufbauer
Received: 9 December 2024
Accepted: 30 June 2025
Published: 6 August 2025

Citation: Serigheli LFC, Bacca S, Marciniak B, Dechoum MS (2025) Prepare for trouble and make it double: Effects of *Carpobrotus acinaciformis* and *Apis mellifera* invasion in floral visitor networks. NeoBiota 100: 1–22. https://doi.org/10.3897/neobiota.100.143555

Copyright: © Luiz F. C. Serigheli et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Global change impacts ecosystem services provided by nature (IPBES 2019). Thus an important goal of biologists and managers is to design strategies to mitigate those impacts. Pollination is an essential ecosystem service that plays a pivotal role not only in sustaining biodiversity, but also in securing food production and main-

taining global climate stability (Vanbergen 2013; Ollerton 2017; Nitharwal et al. 2021). Bees are primary pollinators of unparalleled importance in the intricate web of ecological interactions (Ballantyne et al. 2017), as their role in facilitating the reproduction of flowering plants is key in ecosystem functioning. Studies on the structural and functional attributes of pollination networks are pivotal for understanding the dynamics that underpin ecological resilience and biodiversity conservation (Knight et al. 2018; Hale et al. 2020).

Mutualistic networks, characterized by intricate interactions between species, represent a fundamental aspect of ecosystem processes (Landi et al. 2018). The complex web of relationships within these networks, such as interactions between plants and pollinators, influences ecosystem stability and functioning (Burkle and Alarcón 2011; Burkle et al. 2013; Ballantyne et al. 2017). Metrics such as centrality, connectance, nestedness, and modularity hold important ecological significance for the understanding of pollinator networks (González et al. 2010; Gaiarsa and Bascompte 2022). Each of these metrics represents an ecological aspect, such as abundance of resources provided by species, species acting as generalists or linking subnetworks (centrality measures), ecosystem specialization (nestedness), stability and resilience (modularity and connectance) (González et al. 2010; Gaiarsa and Bascompte 2022). The intricacies of networks provide valuable insights into the mechanisms that govern ecosystem processes, shedding light on how disturbance may reverberate through interconnected systems (Ballantyne et al. 2017; Valido et al. 2019).

Biological invasions can be characterized as a biotic disturbance that poses substantial threats to ecological systems (Weiskopf et al. 2020). Non-native species can affect ecological network metrics such as connectance by altering the number of interactions between species, and nestedness and modularity, by disrupting the interaction preferences of certain species. Invasive species may be specialists or generalists throughout the network (Valido et al. 2019; Parra-Tabla and Arceo-Gómez 2021). Changes in network metrics, such as increased nestedness and reduced modularity, can disrupt native species interactions, leading to local extinctions and cascading effects on mutualistic networks (Morales and Aizen 2002; Gurevitch and Padilla 2004; Bartomeus et al. 2008; Braga et al. 2018). It is thus necessary to explore the far-reaching consequences of invasions on network structures, emphasizing the vulnerability of ecosystems (Aizen et al. 2008; Parra-Tabla and Arceo-Gómez 2021).

Experimental studies and simulations have provided insights into the consequences of invasive species' removal for ecological networks (Brosi et al. 2017; Ollivier et al. 2020), but there is still a lack of studies integrating both approaches to assess the effectiveness of control strategies on pollinator networks (Pyšek and Richardson 2010). Incorporating network analysis and metrics into invasion management strategies has been proposed as a way to achieve a more integrative understanding of long-term ecological dynamics (Ehrenfeld 2010).

Coastal foredunes are dynamic habitats that form along the seaward edge of beaches and represent the first line of defense against coastal erosion. Despite harsh environmental conditions, these habitats support specialized plant and animal communities, including endangered species such as the palm *Butia catarinensis* Noblick & Lorenzi (Falkenberg 1999). Foredunes are often under anthropogenic pressure, including non-native species (Della Bella et al. 2021). *Carpobrotus aci-naciformis* (hereafter referred to by the genus name) is a prominent global invader that has multiple impacts on coastal ecosystems (Roiloa 2019; Rodríguez et al. 2021; Portela et al. 2023) including altering species interactions, and amplifying

competition between pollination interactions and between herbivore interactions (Moragues and Traveset 2005; Núñez González et al. 2023). Additionally, the presence of a species such as *Apis mellifera* (hereafter referred to as honey bees) in invaded ecosystems can alter plant-pollinator interactions and the dynamics of plant communities, affecting the reproduction and diversity of native species (Valido et al. 2019). In spite of the ecological importance of foredunes, we were unable to find studies on the impact of *C. acinaciformis* and *A. mellifera* invasions on ecological networks and biodiversity addressing both observational and experimental studies. We hereby highlight the scarcity of research addressing the impacts of invasive species control on networks and the conservation of crucial interactions in foredunes (Lurgi et al. 2016). Filling in research gaps contributes to inform conservation strategies and enhance our understanding of the intricate relationships between invasive species, ecological networks, and biodiversity.

Here, we studied the interaction networks of bees and native plants on foredunes, with a focus on how these networks shift with (1) *Carpobrotus* invasion, (2) control of *Carpobrotus* and (3) simulated control of invasive honey bees. We hypothesized that *Carpobrotus*, a melitophilous species that provides abundant food resources, and the honey bee, an aggressive generalist forager, would both take on significant roles in interaction networks of pollinators and local plants, affecting network metrics by increasing nestedness and reducing modularity. Additionally, we hypothesized that the mechanical control of *Carpobrotus* and the simulated elimination of the honey bee, both generalist species, would lead to a reduction in nestedness and an increase in modularity.

Material and Methods

Study system

This study was conducted in the Dunas da Lagoa da Conceição Natural Municipal Park, in southern Brazil (27°37'35"S, 48°27'22"W), a protected area covering approximately 707 ha (Fig. 1) of a coastal ecosystem. The local climate is humid subtropical (Cfa) according to the Köppen–Geiger climate classification. The park is a mosaic of several vegetation types, such as sand dunes, coastal scrub, low forests, and wetlands. Beginning on the beach on open sand, the vegetation transitions to foredunes, then to interior mobile, semi-fixed and fixed dunes, in between which lie low areas that may be dry, damp or periodically flooded, forming temporary or permanent pools (Guimarães 2006). This study focused on foredunes, characterized by low vegetation and subshrubs, featuring plants adapted to conditions marked by high variability in factors such as wind, light, and salinity (Guimarães 2006). The park holds historical, archaeological, and social significance, attracting tourists and the local community.

Data collection

The fieldwork was carried out between the months of October and January in two consecutive years, during the peak flowering season of native plants in the study area (Guimarães 2006). In year 1 (October 2021 – January 2022), we collected bees and flowers in two areas (A and B): one invaded by *Carpobrotus* – Invaded (27°41'42.1"S, 48°29'10.9"W – 27°41'29.9"S, 48°28'57.3"W) and Uninvaded

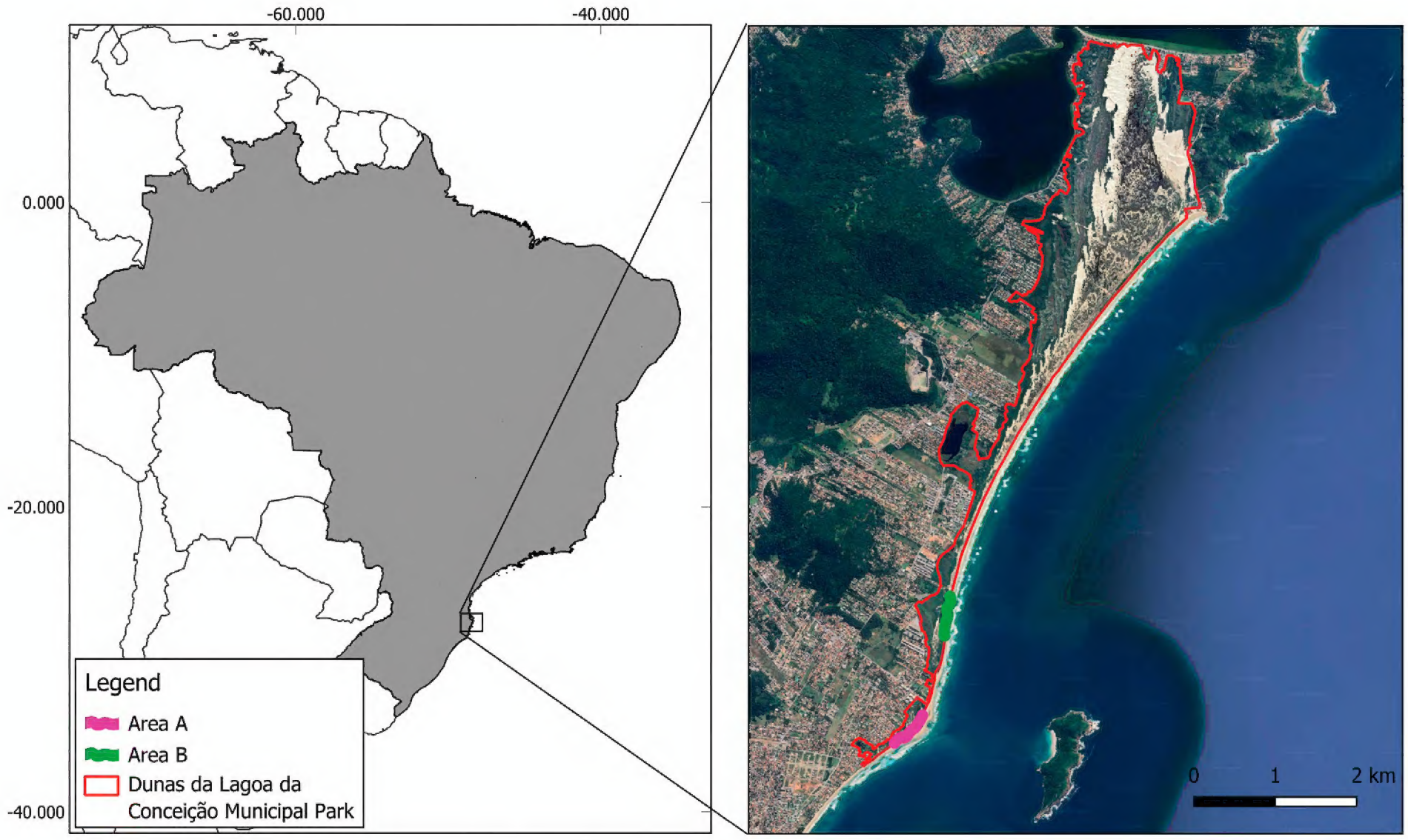

Figure 1. Brazil map with detail of the Dunas da Lagoa da Conceição Natural Municipal Park. Location and limits of the Dunas da Lagoa da Conceição Natural Municipal Park in Florianópolis, Santa Catarina (red line), and sampling areas: (pink – A) area invaded by *Carpobrotus* and later managed; (green –B) area uninvaded by *Carpobrotus* year 1 and year 2.

(27°40'53.7"S, 48°28'47.0"W – 27°40'36.9"S, 48°28'44.6"W). Each sampling area measured approximately 500 m in length by 20 m in width, totaling 10,000 m^2 per area. The areas were approximately 1.2 km apart. In year 2 (October 2022 – January 2023), the same areas were resampled after the mechanical removal of all *Carpobrotus* plants in June and July of 2022 (aprox. 500m^2). The formerly invaded area was then renamed as Managed (where *Carpobrotus* was mechanically removed), while Uninvaded was maintained, in year 2. Mechanical control of *Carpobrotus* involved the manual removal of stolons and shoots with roots, followed by disposal. The plant residues were collected by the municipal solid waste authority and sent for composting.

We conducted active searches to collect bees on flowers and inflorescences of all species based on an adapted version of the method by Sakagami and Fukuda (1973). This method consists of systematically collecting bees with hand nets during fixed time intervals while recording floral associations, environmental conditions, and foraging behavior, enabling standardized assessment of data. We adapted the method because foraging behavior was not relevant to our study. Each area was sampled once a month between 8:30 am and 3:30 pm with similar environmental conditions of temperature and wind. Bee nets were used to capture individuals visiting flowers and inflorescences of herbs and shrubs. The bees collected were euthanized using ethyl acetate chambers, then stored in a freezer, fixed and identified (Silveira et al. 2002; Almeida et al. 2012). The flowering plant species on which bees were recorded were identified by local taxonomists linked to the Federal University of Santa Catarina Herbarium, either based on photographs or on collected material. The identification of both plant and bee species was made at the lowest taxonomic level possible, provided at Appendix 1 with both species list per area (Tables A1, A2).

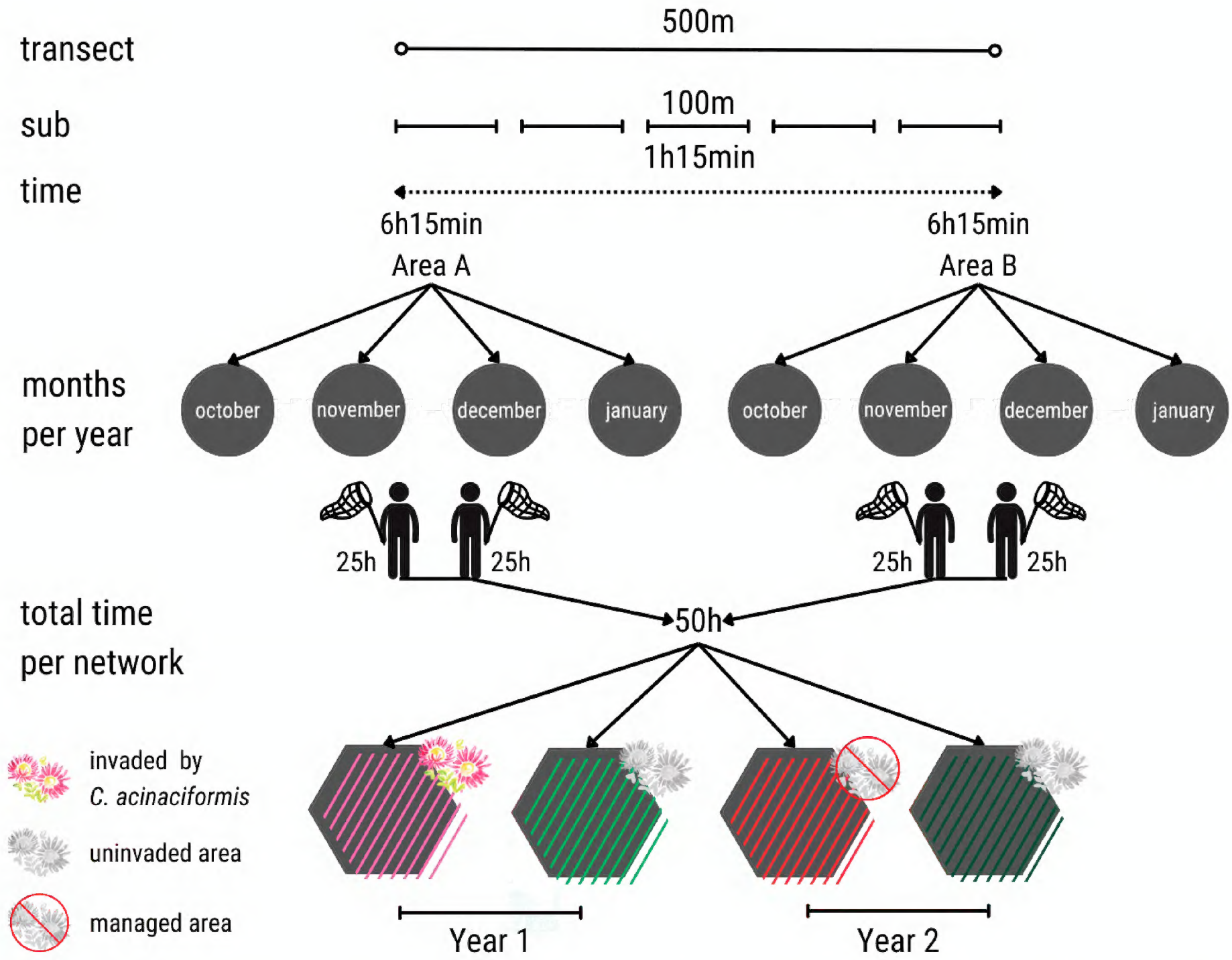

Figure 2. Sampling methodology. Collection by two individuals in two areas (500m/6h15min/day) subdivided into sub-areas (100m/75min/day) in the months of October, November, December, and January; before and after *Carpobrotus* control. Schematic representation of the four interaction networks selected for sampling during the project (hexagons): Invaded; Uninvaded year 1; Managed; Uninvaded year 2. Source: Serigheli, L. F. C.

In the process of sampling, each area was divided into five sub-areas of 100 × 20 m. The sampling sequence of sub-areas was determined by daily random selection. The time of data collection in each sub-area was approximately 1 hour and 15 minutes, totaling approximately 6 hours and 15 minutes of active search per day per area per month. All collection activities were conducted by two observers, which doubled the sampling effort and accounted for approximately 100 hours of collection, or 50 hours per network (Fig. 2).

Data analysis

The data on plant and bee species were organized into quantitative matrices for analysis, with rows representing bee species, columns, plant species, and the number of interactions represented by the amounts of individuals collected in each interaction. We then generated networks, where plants and bees are represented as nodes, and interactions are represented by lines. The thickness of lines represents the number of interactions – the thicker the line, the higher the number of interactions.

We compared the networks in pairs, as in year 1: Invaded vs Uninvaded year 1; year 2 (after mechanical control of *Carpobrotus*): Invaded vs Managed; Invaded vs Unin-

vaded year 2; Managed vs Uninvaded year 2. General metrics of ecological interaction networks were assessed for each network, including (a) connectance (connectance; Dormann et al. 2008); (b) nestedness and respective contribution (weighted NODF; Almeida-Neto and Ulrich 2011); (c) modularity (DIRTLPAwb+ algorithm; Beckett 2016); (d) centrality (centrality measures; González et al. 2010); and (e) Interaction Strength Asymmetry (ISA; Dormann et al. 2008). Given the lack of replication on the study site, r2d null models were employed to determine the significance of the results obtained (null.t.test with 999 randomizations – Dormann et al. 2008). Interaction strength asymmetry varies between –1 and 1, with positive values indicating high dependence of an animal on a plant species, and negative values indicating the opposite (Blüthgen et al. 2007). At the species level, we assessed the asymmetry of species interactions using the push-pull index, which indicates the direction of interaction asymmetry based on dependency; positive values indicate that a species more strongly affects the species of the other level with which it interacts than vice-versa, therefore being a central and resourceful species ("pusher"), while negative values indicate that a species is more strongly affected by interaction partners than affects them, therefore more vulnerable and susceptible to decline and/or extinction ("being pulled") (Vázquez et al. 2007).

Recognizing the pervasive influence of *A. mellifera*, we conducted removal simulations using all species matrices to assess the potential impact of eliminating honey bees in network dynamics. In the simulations, we compared general network metrics in pairs: Invaded vs Invaded without *A. mellifera*, Uninvaded year 1 vs Uninvaded year 1 without *A. mellifera*, Managed vs Managed without *A. mellifera*, and Uninvaded year 2 vs Uninvaded year 2 without *A. mellifera*, in order to provide a comparative perspective on the role of the invasive bee in shaping network structure.

Data analyses were performed using the R environment packages version 4.3.1 (R Core Team 2023): bipartite (Dormann et al. 2009) and vegan (Oksanen et al. 2020).

Results

General descriptive results

We collected and identified 1,672 bees of 29 species in interaction with 31 plant species. A total of 262 interactions were recorded in the period of the study. There was no significant variance in connectance between networks, which only increased very slightly in the Managed network (M). The highest number of interactions was observed in the uninvaded network in year 1 (U1), with 23% more interactions on average in comparison with the other networks. This network also contained the highest number of plant species. On the other hand, the number of bee species was larger in the invaded network (I) (Table 1). Nestedness and modularity were higher in the invaded network compared with the uninvaded and managed networks (Invaded vs Uninvaded year 1; and Invaded vs Managed). The invasive plant *Carpobrotus* and the invasive honey bee both occupied the central roles in the invaded network (I) (Fig. 3a, c).

Impacts of the invasive species on network dynamics

Invasive *Carpobrotus acinaciformis* was the plant species with the highest abundance of bee visitors (128 bees), representing 24% of the interactions in the network and occupying the central role (Fig. 3a). In addition, the highest nestedness and lowest modularity were observed in the presence of *Carpobrotus* in comparison with the other scenarios

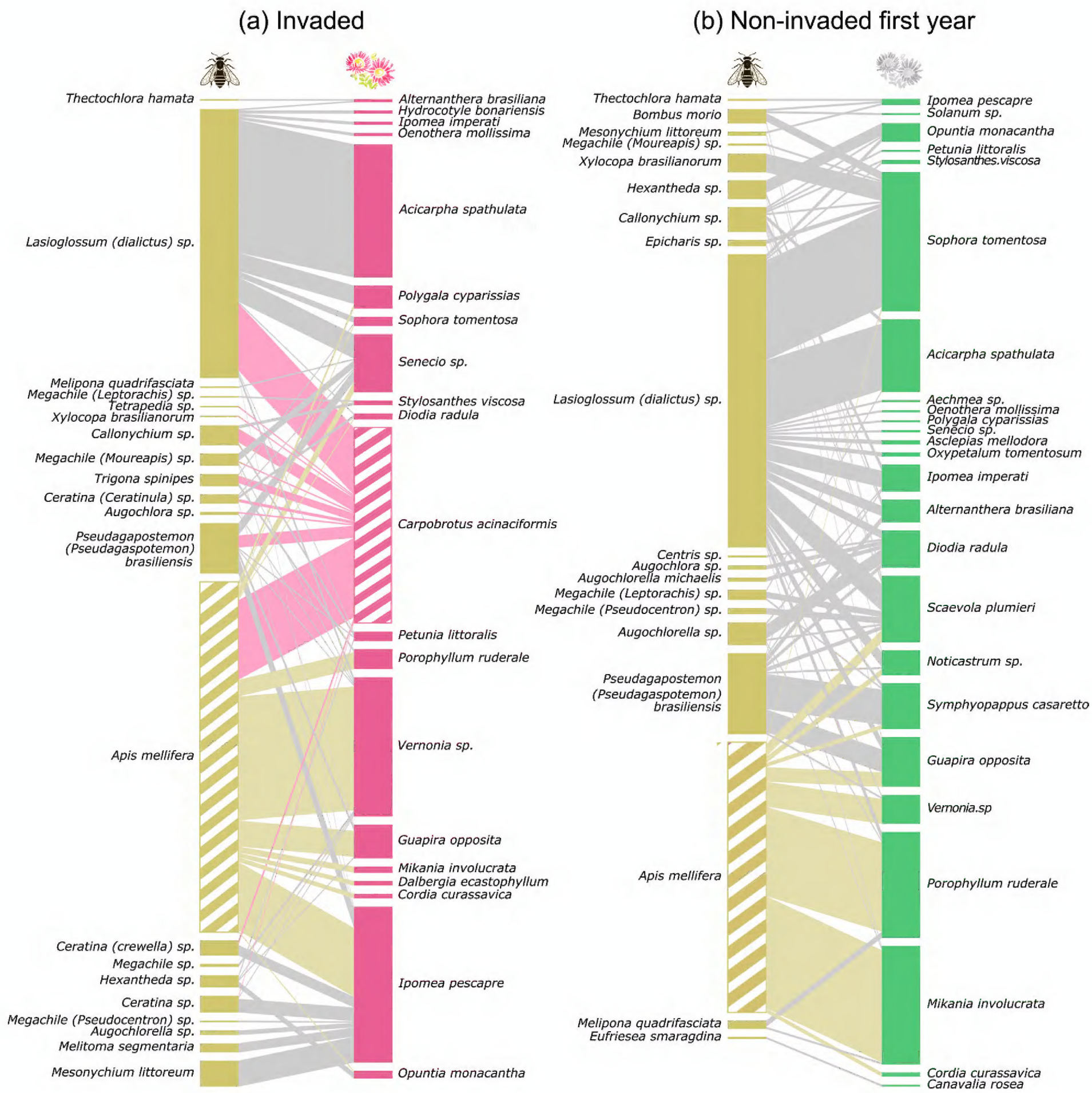

Figure 3. Bee-plant networks in the two sampling areas over the period of two years of the study. Bee-plant interaction networks in the Dunas da Lagoa da Conceição Natural Municipal Park (Florianópolis, Santa Catarina), southern Brazil, between October, 2021 – January, 2022, and October, 2022 – January, 2023. Detailed overview of the four bipartite interaction networks. Bee species are shown on the left side in grayish-yellow, and plant species on the right, colored according to the plant community: **a.** Invaded (pink); **b.** Uninvaded – year 1 (light green); **c.** Managed (red), and **d.** Uninvaded – year 2 (dark green). Lined bars represent the two invasive species, and color links the respective interactions (*Carpobrotus acinaciformis* – pink, *Apis mellifera* – ocre).

in which it was absent (Invaded vs Uninvaded year 1, Invaded vs Managed, Invaded vs Uninvaded year 2). *Carpobrotus* was by far the plant species that most contributed to nestedness (3.125), followed by the native creeper *Ipomea pes-caprae* (2.344).

The honey bee plays a significant role across all networks, emerging as the most abundant in three of the four networks (Fig. 3a, c, d), and ranking second in abundance in the network in year 1 (Fig. 3b). Furthermore, honey bees provided a high contribution to nestedness and degree centrality across all networks. It was also the spe-

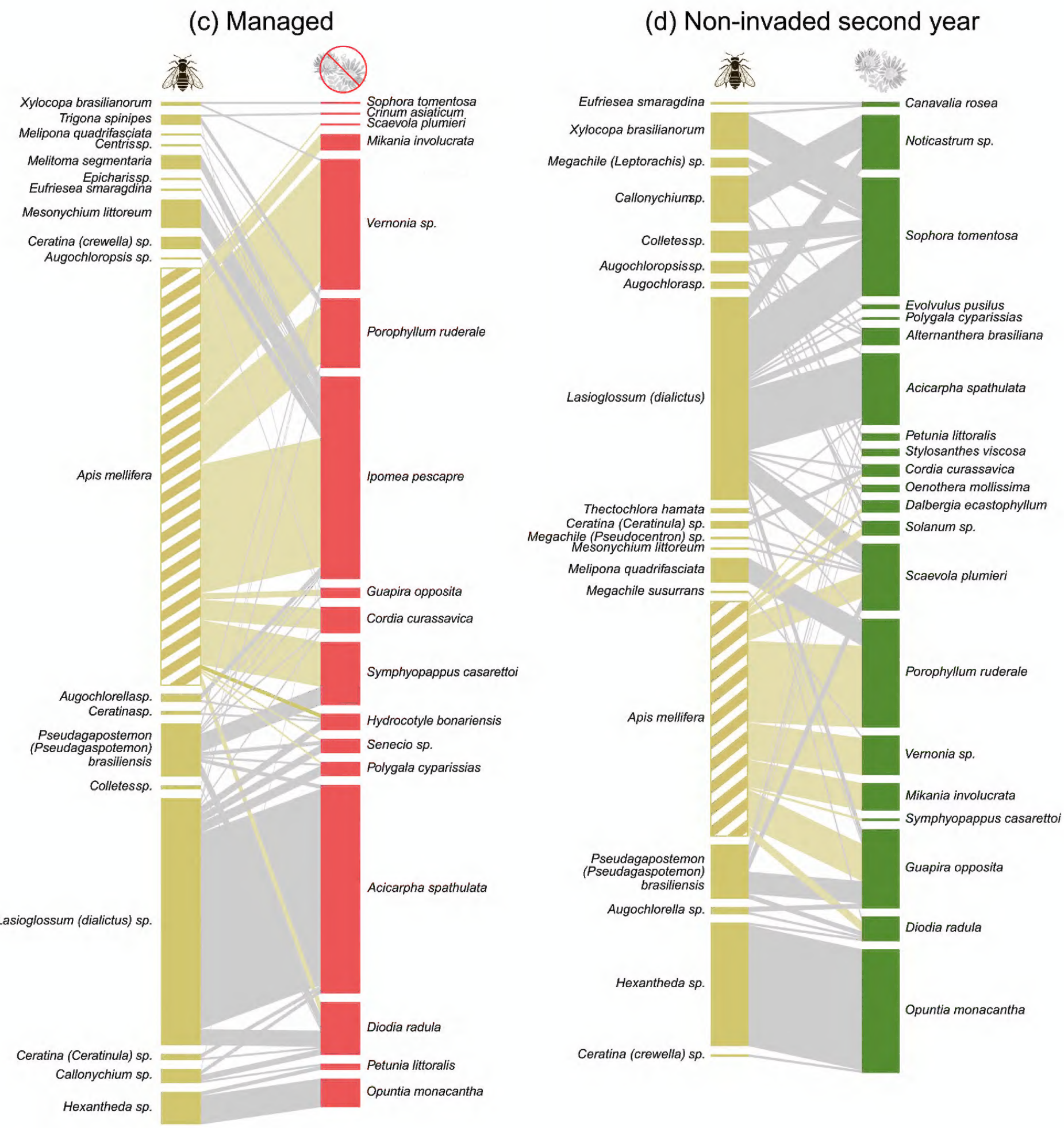

Figure 3. Continued.

Table 1. Overview of bee-plant interaction networks.

Location	No. Indivs.	Interactions links	Bee species	Plant species	Ns*	C*	Mo*	ISA
Invaded	538	67	21	20	48.80	0.16	0.38	-0.08
Uninvaded1	383	76	19	25	44.37	0.16	0.49	-0.05
Managed	424	56	19	17	36.69	0.17	0.45	-0.05
Uninvaded2	327	63	19	21	28.65	0.16	0.55	-0.04

Overview of the total number of individuals bees collected (No. Indivs.), interactions links, the number of bee species and plant species, nestedness (N), connectance (C), modularity (Mo) and interaction strength asymmetry (ISA) in each location. *indicate that null models were significant for each of the values and are provided in the Appendix 1 for a more comprehensive analysis (Fig. A1).

cies that most contributed to nestedness in both the invaded and managed networks, with a contribution to nestedness of 3.895 in the invaded network (Fig. 3a). Even though honey bees contributed the most to nestedness in all networks, its impact in the managed network (Fig. 3c) was reduced after the removal of *Carpobrotus*. Although it continued to have a strong influence, the nestedness value decreased to 2.601.

All *Interaction Strength Asymmetry* (ISA) values were negative, demonstrating that plants are more dependent on bees than otherwise. The highest value was recorded in the invaded network (I), which largely decreased after removal of *Carpobrotus*, becoming closer to the networks (Invaded vs Managed; Invaded vs Uninvaded year 1; Invadaded vs Uninvaded year 2). Furthermore, *Carpobrotus* is the second most influential species in the push-pull index in the invaded network, ranking just below *I. pes-caprae*. The honey bee was the most influential bee species in the push-pull index in all networks. Following the management of *Carpobrotus*, two plant species that were pullers in the invaded network, *Acicarpha spathulata* and *Porophyllum ruderale*, assumed the role of pushers in the new managed network (Invaded vs Managed), replicating their roles in the uninvaded networks (Invaded vs Uninvaded year 1, Invaded vs Uninvaded year 2) (Fig. 4).

Exploring network dynamics without *Apis mellifera*

The removal of honey bees from the network matrix reduced the total number of bees sampled by 39% (1,014 of 1,672 bee specimens). Although the number of plant species with interactions was not reduced, the number of interactions/links was reduced by 17% on average in the simulation of honey bees' elimination in all networks. It is important to note that all specific metrics evaluated for networks were similar when compared within the same year (Invaded without *A. mellifera* vs Uninvaded year 1 without *A. mellifera*, Managed without *A. mellifera* vs Uninvaded year 2 without *A. mellifera*), but diverged upon comparison within each network in years 1 and 2 (Invaded without *A. mellifera* vs Managed without *A. mellifera*, Uninvaded year 1 without *A. mellifera* vs Uninvaded year 2 without *A. mellifera*) (Fig. 5 a, b). The results obtained are presented in Table 2.

Impact on nestedness, connectance, and modularity

The removal of honey bees resulted in visible changes between the controlled simulation and the actual scenario (M vs. Ma), with a reduction of nestedness and an increase in modularity in the managed site. This shows that the metrics of the managed site became similar to the uninvaded site in year 2 (Managed without *A. mellifera* vs Uninvaded year 2 without *A. mellifera*). This comes to show that the network would be more likely to have the same traits and behavior of the uninvaded areas if both invasive species were eliminated. Besides, *Carpobrotus* retained its central role in nestedness even in the absence of honey bees, indicating its resilience and significance in shaping network dynamics.

All the ISA values were negative and closer to 0 compared with the scenario with honey bees, demonstrating that plants are more dependent on bees than otherwise, but less than before the honey bee was removed from the network analysis. ISA (Fig. 6) values between all the networks were far more similar to each other compared with the values generated with the presence of honey bees. Furthermore, *Lasioglossum* (*dialictus*) sp. became the most influential species in the push-pull index in all the networks.

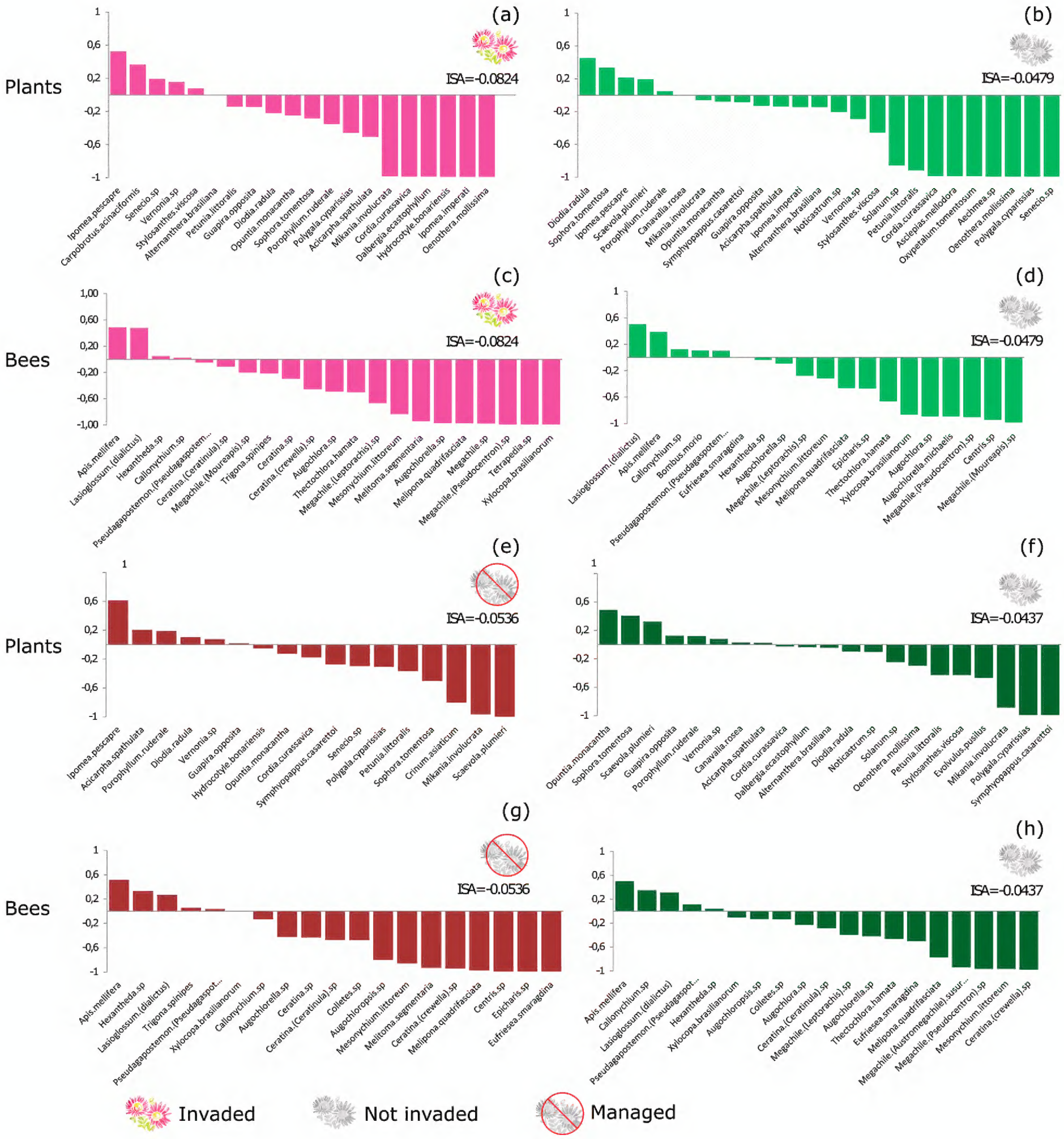

Figure 4. Interaction push-pull index and Interaction Strength Asymmetry in bee-plant interaction networks. Values from networks in the Dunas da Lagoa da Conceição Natural Municipal Park (Florianópolis, SC, Brazil), southern Brazil, between October 2021 – January, 2022, and October, 2022 – January, 2023. **a, c.** Invaded network; **b, d.** Uninvaded network year 1; **e, g.** Managed network; **f, h.** Uninvaded network year 2. Interaction push-pull ranges from -1 (pullers) to 1 (pushers). Bars represent plants and bee species.

Discussion

Our results provide a detailed assessment of the ecological effects of the presence and elimination of the invasive plant *C. acinaciformis* and removal simulation of invasive bee *A. mellifera*. Notably, the network with *Carpobrotus* had higher nestedness and lower modularity compared with networks without the invasive plant. In the managed network nestedness decreased and modularity increased

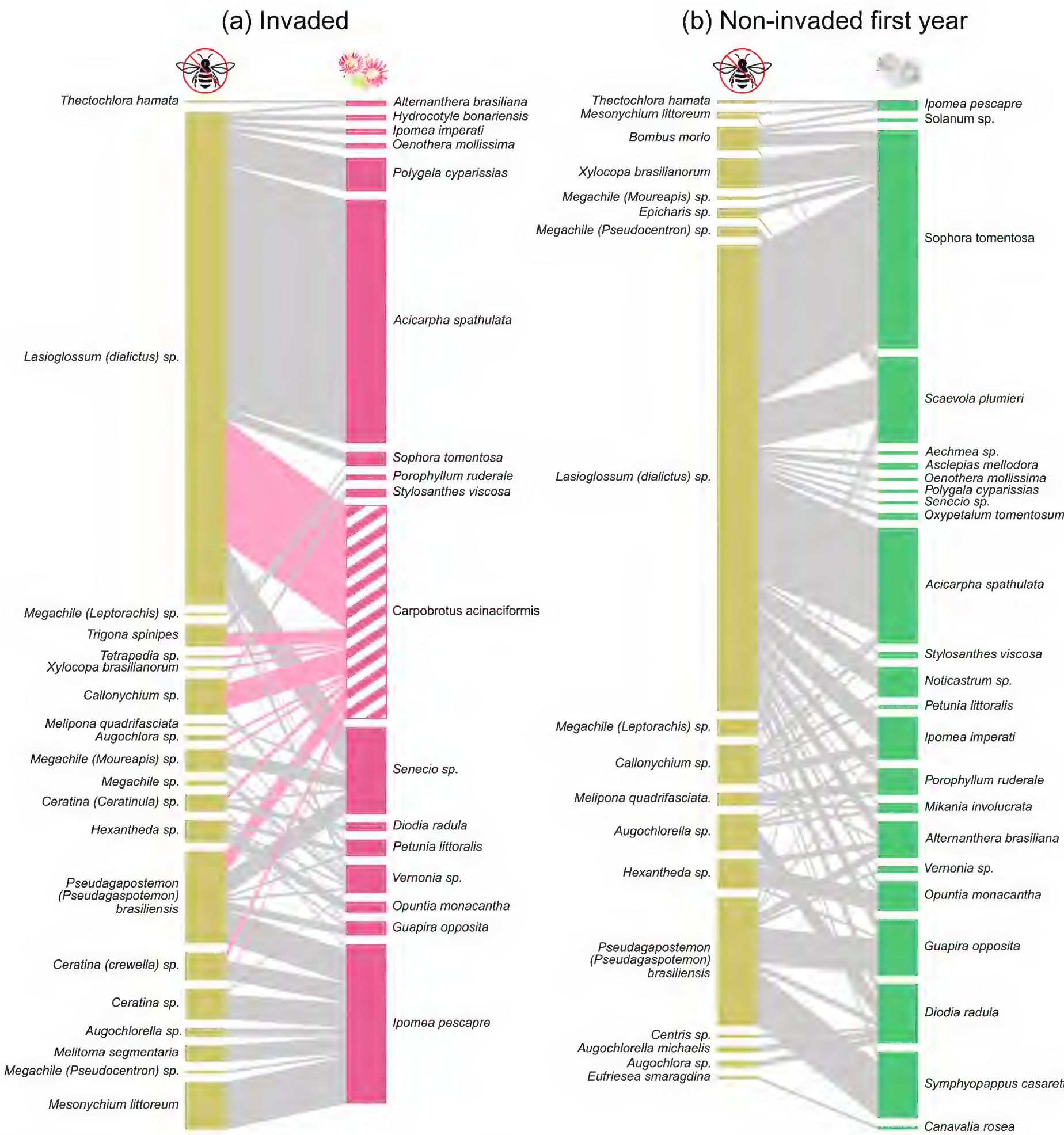

Figure 5. Simulation of bee-plant interaction networks without honey bees in the two sampling areas in the two years of the study. Bee-plant interaction networks without honey bees in the Dunas da Lagoa da Conceição Natural Municipal Park (Florianópolis, Santa Catarina), southern Brazil, between October, 2021 – January, 2022, and October, 2022 – January, 2023. Detailed overview of the four bipartite interaction networks. Bee species are shown on the left side in grayish-yellow all without *A. mellifera*, and plant species on the right, colored according to the plant community: **a.** Invaded (pink); **b.** Uninvaded – year 1 (light green); **c.** Managed (red), and **d.** Uninvaded – year 2 (dark green). Lined bars represent invasive plant species and color links, respective interactions (*C. acinaciformis* – pink).

in comparison to the invaded and uninvaded networks. The same was observed in the simulated elimination of honey bees from the networks, which resulted in decreased nestedness and modularity. This corroborates our hypothesis that both invasive species, *Carpobrotus* and honey bees, increase nestedness and reduce modularity in native plant-pollinator networks. Our findings potentially indicate the start of a shift towards a more stabilized and specialized system, with implications for the ecological resilience of the managed network in the long term. We highlight

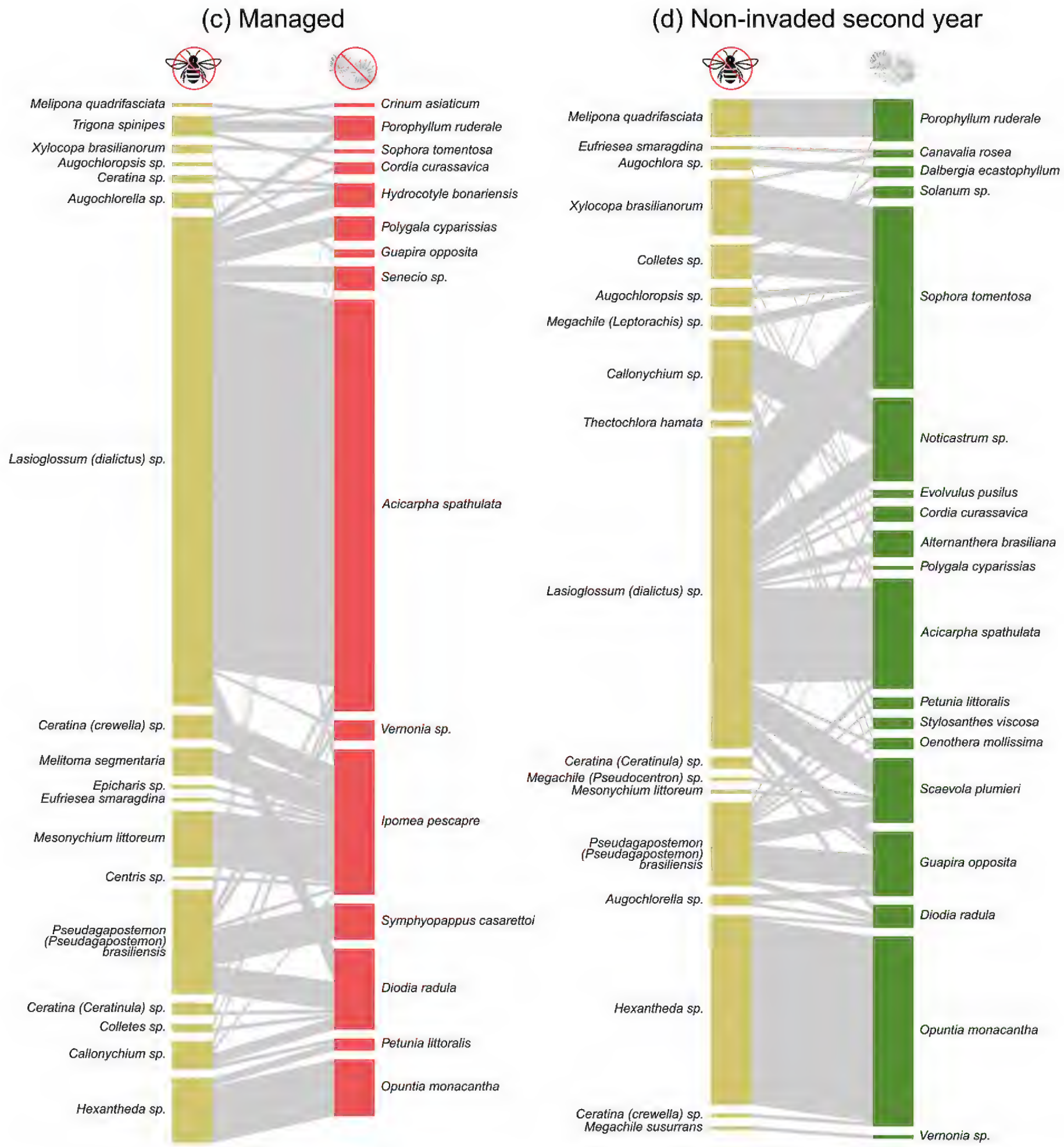

Figure 5. Continued.

Table 2. Bee-plant interaction networks without *Apis mellifera*.

Location	No. Indivs.	Interactions links	Bee species	Plant species	N*	C*	Mo*	ISA
Invaded	309	54	20	17	42.88	0.16	0.39	-0.05
Uninvaded1	253	67	18	24	45.69	0.16	0.38	-0.02
Managed	220	44	18	15	29.03	0.16	0.52	-0.01
Uninvaded2	232	53	18	19	24.24	0.16	0.55	-0.02

Overview of the total number of individual bees collected (No. indivs.), interactions links, the number of bee species and plant species, nestedness (N), connectance (C), modularity (Mo) and interaction strength asymmetry (ISA) in each location. *indicate that null models were significant for each of the values and are provided in Appendix 1 for a more comprehensive analysis (Fig. A2).

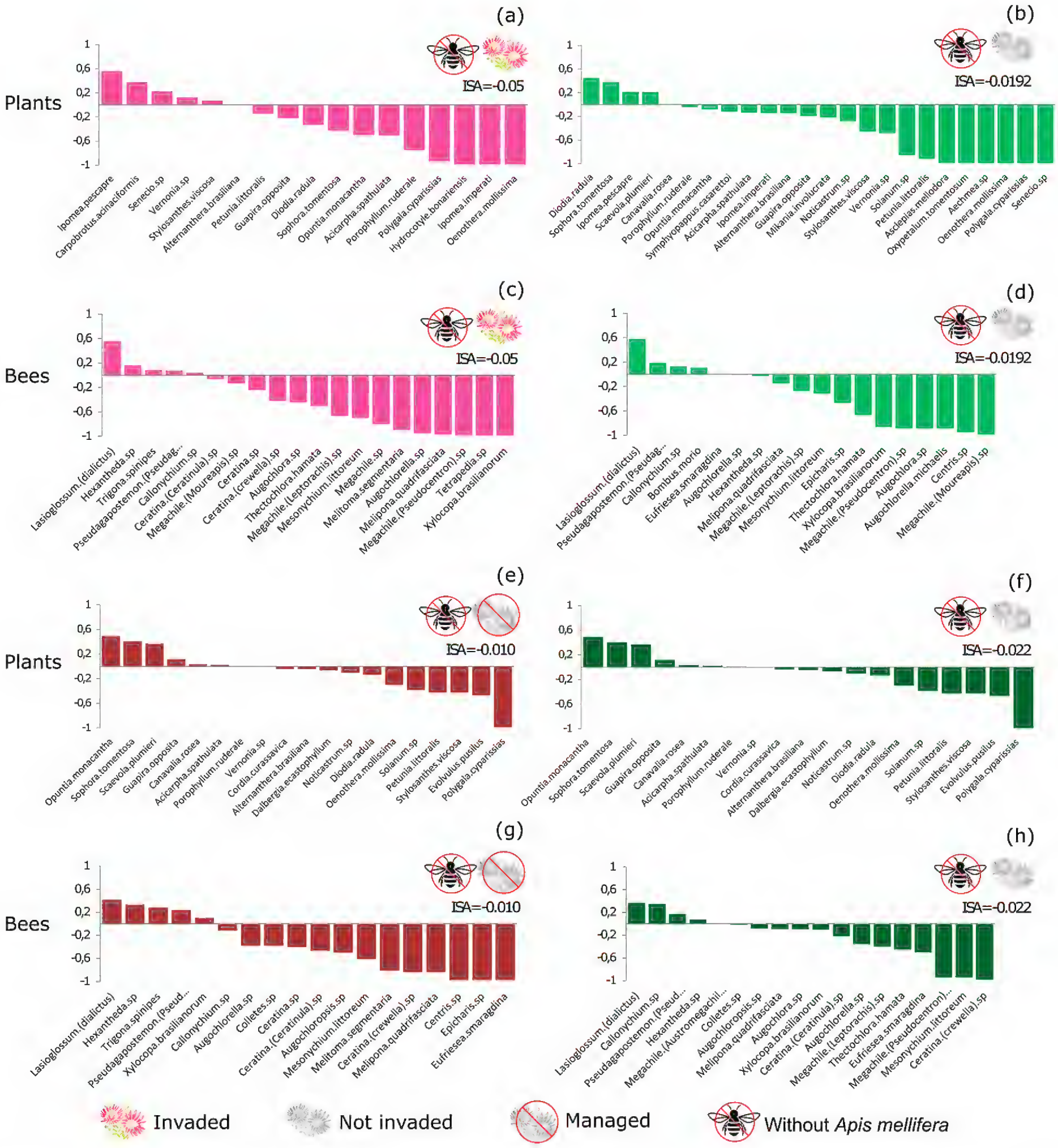

Figure 6. Interaction push-pull index and interaction strength asymmetry in bee-plant interaction networks in the simulation of *A. mellifera* elimination. Values from networks of bee-plant interaction networks without honey bees (simulation) in the Dunas da Lagoa da Conceição Natural Municipal Park (Florianópolis, SC, Brazil), southern Brazil, between October, 2021 and January, 2023. **a, c.** Invaded network; **b, d.** Uninvaded network year 1; **e, g.** Managed network; **f, h.** Uninvaded network year 2. Interaction push-pull ranges from -1 (pullers) to 1 (pushers). Bars represent plant and bee species (lower level).

that monitoring is essential, and that *Carpobrotus* might require repeated control interventions for this system change to become permanent over time.

These findings suggest a significant influence of invasive plants on network structure, causing changes via competition for mutualists with native species, disrupting coevolution interactions, and modifying network metrics – ultimately reducing native biodiversity and weakening ecosystem resilience (Moragues and Traveset 2005;

Rodríguez et al. 2021). This leads to increased nestedness and centrality, and corroborates the fact that the control of invasive species can positively impact network structure and ecological interactions. The distinct roles of both invasive species were clear, as both contributed significantly to network structure in central roles, attracting interactions with native species and changing species dynamics in the long term. This result emphasizes the complex interplay of invasive species in ecological systems, as well as the potential for amplified impacts in the presence of more than one invasive species (Invasive Meltdown Hypothesis – process by which two or more non-native species facilitate each other establishment or exacerbate each other impact on native species (Simberloff and Von Holle 1999; Beavon and Kelly 2012; Bartomeus et al. 2008; Aizen et al. 2008). The elimination of *Carpobrotus* and the simulated removal of honey bees from the networks offers insights into potential shifts in network dynamics, with native species of plants and bees taking over central roles, as well as native plants changing roles from pullers to pushers (Brosi et al. 2017; Núñez González et al. 2023). Still, the results emphasize that, once assuming central roles, native species attract native pollinators, increase network connectance and ecosystem resilience in the long term (Gaiarsa and Bascompte 2022).

Our findings are aligned with existing literature on the ecological impacts of invasive species, particularly in the context of pollination networks. Studies on *Carpobrotus* have reported impacts on networks, both positive, for providing resources and attracting native pollinator species, and negative, for increasing competition between native plant species and reducing network connectance. These findings highlight the need to consider specific ecological contexts (Moragues and Traveset 2005; Bartomeus et al. 2008; Rodríguez et al. 2021; Núñez González et al. 2023). Also, the strong influence of honey bees observed in our study echoes similar findings in recent work on pollination networks in the Canary Islands (Valido et al. 2019), where its contribution to nestedness in the invaded network was the highest of all species. This result corroborates ecological impacts and enables us to clearly see the effect of the *invasive meltdown hypothesis* (Bartomeus et al. 2008; Aizen et al. 2008).

The influence of invasive species on pollination networks has been a subject of increasing interest in ecological research. Understanding these dynamics is important in the development of effective conservation and management strategies (Gaiarsa and Bascompte 2022). Several limitations must be acknowledged in our study. The lack of areas for replication in the Natural Municipal Park of Dunas da Lagoa da Conceição constrained the generalizability of our findings; to address this, we used null models to assess and validate the observed patterns (Dormann et al. 2009). Additionally, the comparison between networks in years 1 and 2 introduced potential temporal and bee-population variations. To minimize these effects, sampling was conducted under similar weather conditions and in the same season across both years. We acknowledge that the time allowed for ecosystem recovery following invasive plant removal was relatively short. However, our focus was on plant species composition, rather than plant species cover or abundance, as our primary objective was to build the plant–pollinator networks and assess compositional changes linked to management. Although a two-year study limits our ability to assess long-term impacts, it nonetheless allowed us to detect immediate shifts in network structure following the removal of the invasive plant species. These early responses provide valuable insights into the short-term ecological consequences of invasion management. Future studies with long-term monitoring and replicated sites will be essential to deepen and confirm these findings. Finally, the simulated

removal was the only viable approach to evaluate the hypothetical absence of *Apis mellifera*, as eradication of this widespread invader was not feasible.

Future studies may also delve into specific mechanisms through which *Carpobrotus* and honey bees influence network structure, exploring potential cascading effects on native flora and fauna. Long-term monitoring and experimental manipulations in replication areas would provide valuable insights into the resilience and adaptive capacity of ecological networks. In this respect, we recommend prioritizing the use of native plant species that behave as pushers and occupy a central role in pollination networks in ecological restoration, such as *Ipomea pes-caprae*, *Sophora tomentosa*, and *Diodia radula*. Moreover, we recognize the need for more work in the conservation and monitoring of key native pollinator species, such as *Lasioglossum* (*dialictus*) sp. Furthermore, there is a need for continued research on effective invasive species management strategies and their consequences on ecological interactions. Integrating findings from multiple studies across different ecosystems and invasive species will contribute to a more comprehensive understanding of the broader ecological implications of biological invasions (Lurgi et al. 2016), and the development of targeted conservation efforts.

Conclusion

This study contributes to the expanding body of ecological knowledge on the intricate dynamics of ecological interaction pollination networks in the presence of invasive non-native species. The insights generated by our study contribute to the theoretical advancement of invasion science and hold pragmatic implications for biodiversity conservation in foredunes in coastal ecosystems, as well as for native bee and plant species. By dissecting the multifaceted interactions influenced by invasive species, the results of our study contribute to the understanding of ecosystem resilience and adaptation mechanisms.

Moreover, the knowledge generated by our study is an addition to the scientific understanding of invasive species dynamics and their repercussions on ecological interaction networks. As scientific endeavors continue to unravel the complexities of invasive species ecology, the findings from this study inform decision-makers and conservation practitioners on the use of key native species for restoration and conservation. This study contributes to the scientific knowledge on the effects of *C. acinaciformis* and *A. mellifera* invasion and their control in bee-plant networks and native species in foredunes, increasing the applicability of evidence-based biodiversity management and conservation plans, while emphasizing the need for adaptive strategies in mitigating the impacts of invasive species on ecosystem dynamics.

Acknowledgments

The plants collected were identified with help from Everton Richetti and Leonardo Arthur Keller Neto, students at the Herbário Flor, Federal University of Santa Catarina, Brazil.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

LFCS and BM respectively scholarships from the Programa de Bolsas Universitárias de Santa Catarina (UNIEDU) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) [Financial code 001], respectively. MSD received financial support from CNPq (Research Productivity Scholarship – Bolsa de Produtividade em Pesquisa – # 302880/2022-4).

Author contributions

Conceptualization: LFCS, MSD. Data curation: SB, LFCS. Formal analysis: BM, LFCS. Methodology: MSD, LFSD. Project administration: LFCS. Supervision: MSD. Writing – original draft: LFCS. Writing –review and editing: MSD, BM.

Author ORCIDs

Luiz F. C. Serigheli https://orcid.org/0000-0001-9993-1726
Sofia Bacca https://orcid.org/0000-0002-0575-814X
Brisa Marciniak https://orcid.org/0000-0002-0507-723X
Michele S. Dechoum https://orcid.org/0000-0002-3484-2498

Data availability

All of the data that support the findings of this study are available in the main text.

References

Aizen MA, Morales CL, Morales JM (2008) Invasive Mutualists Erode Native Pollination Webs. PLoS Biology 6: e31. https://doi.org/10.1371/journal.pbio.0060031

Almeida LM, Ribeiro-Costa CS, Marinoni L (2012) Coleta, montagem, preservação e métodos para estudo. In: Rafael JA, Melo GAR, de CJB, Casari SA, Constantino R (Eds) Insetos do Brasil: Diversidade e Taxonomia. Holos, Ribeirão Preto, 175–190.

Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. Environmental Modelling & Software 26: 173–178. https://doi.org/10.1016/j.envsoft.2010.08.003

Ballantyne G, Baldock KCR, Rendell L, Willmer PG (2017) Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. Scientific Reports 7: 8389. https://doi.org/10.1038/s41598-017-08798-x

Bartomeus I, Vilà M, Santamaría L (2008) Contrasting effects of invasive plants in plant–pollinator networks. Oecologia 155: 761–770. https://doi.org/10.1007/s00442-007-0946-1

Beavon MA, Kelly D (2012) Invasional meltdown: Pollination of the invasive liana Passiflora tripartita var. mollissima (Passifloraceae) in New Zealand. New Zealand Journal of Ecology 100–107. http://www.jstor.org/stable/24060879

Beckett SJ (2016) Improved community detection in weighted bipartite networks. Royal Society Open Science 3: 140536. https://doi.org/10.1098/rsos.140536

Blüthgen N, Menzel F, Hovestadt T, Fiala B, Blüthgen N (2007) Specialization, constraints, and conflicting interests in mutualistic networks. Current Biology 17(4): 341–346. https://doi.org/10.1016/j.cub.2006.12.039

Braga RR, Gómez-Aparicio L, Heger T, Vitule JRS, Jeschke JM (2018) Structuring evidence for invasional meltdown: Broad support but with biases and gaps. Biological Invasions 20: 923–936. https://doi.org/10.1007/s10530-017-1582-2

Brosi BJ, Niezgoda K, Briggs HM (2017) Experimental species removals impact the architecture of pollination networks. Biology Letters 13: 20170243. https://doi.org/10.1098/rsbl.2017.0243

Burkle LA, Alarcón R (2011) The future of plant–pollinator diversity: Understanding interaction networks across time, space, and global change. American Journal of Botany 98: 528–538. https://doi.org/10.3732/ajb.1000391

Burkle LA, Marlin JC, Knight TM (2013) Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. Science 339: 1611–1615. https://doi.org/10.1126/science.1232728

Della Bella A, Fantinato E, Scarton F, Buffa G (2021) Mediterranean developed coasts: What future for the foredune restoration? Journal of Coastal Conservation 25: 49. https://doi.org/10.1007/s11852-021-00838-z

Dormann C, Gruber B, Fründ J (2008) Introducing the bipartite Package: Analyzing Ecological Networks. R News 8. https://journal.r-project.org/articles/RN-2008-010/

Dormann C, Fründ J, Blüthgen N, Gruber B (2009) Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. The Open Ecology Journal 2: 7–24. https://doi.org/10.2174/1874213000902010007

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics 41(1): 59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650

Falkenberg DB (1999) Aspectos da flora e da vegetação secundária da restinga de Santa Catarina, Sul do Brasil. INSULA Revista de Botânica 28: 1–30. https://periodicos.ufsc.br/index.php/insula/article/view/21771

Gaiarsa MP, Bascompte J (2022) Hidden effects of habitat restoration on the persistence of pollination networks. Ecology Letters 25: 2132–2141. https://doi.org/10.1111/ele.14081

González AMM, Dalsgaard B, Olesen JM (2010) Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity 7: 36–43. https://doi.org/10.1016/j.ecocom.2009.03.008

Guimarães TB (2006) Florística e fenologia reprodutiva de plantas vasculares na restinga do Parque Municipal das Dunas da Lagoa de Conceição. MS Thesis. Universidade Federal de Santa Catarina (Florianópolis). https://tede.ufsc.br/teses/PBVE0046.pdf

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends in Ecology & Evolution 19(9): 470–474. https://doi.org/10.1016/j.tree.2004.07.005

Hale KRS, Valdovinos FS, Martinez ND (2020) Mutualism increases diversity, stability, and function of multiplex networks that integrate pollinators into food webs. Nature Communications 11: 2182. https://doi.org/10.1038/s41467-020-15688-w

IPBES [Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services] (2019) Global assessment report on biodiversity and ecosystem services. Brondizio ES, Settele J, Díaz S, and Ngo HT (Eds) IPBES secretariat, Bonn, Germany, 1148 pp. https://doi.org/10.5281/zenodo.3831673

Knight TM, Ashman T-L, Bennett JM, Burns JH, Passonneau S, Steets JA (2018) Reflections on, and visions for, the changing field of pollination ecology. Ecology Letters 21: 1282–1295. https://doi.org/10.1111/ele.13094

Landi P, Minoarivelo HO, Brännström Å, Hui C, Dieckmann U (2018) Complexity and stability of ecological networks: A review of the theory. Population Ecology 60: 319–345. https://doi.org/10.1007/s10144-018-0628-3

Lurgi M, Wells K, Kennedy M, Campbell S, Fordham DA (2016) A Landscape Approach to Invasive Species Management. PLoS One 11(7): e0160417. https://doi.org/10.1371/journal.pone.0160417

Moragues E, Traveset A (2005) Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. Biological Conservation 122: 611–619. https://doi.org/10.1016/j.biocon.2004.09.015

Morales CL, Aizen MA (2002) Does Invasion of Exotic Plants Promote Invasion of Exotic Flower Visitors? A Case Study from the Temperate Forests of the Southern Andes. Biological Invasions 4: 87–100. https://doi.org/10.1023/A:1020513012689

Nitharwal M, Rolania R, Jatav HS, Chandra K, Khan MA, Kumawat S, Attar SK, Dhaka SR (2021) Pollinators: Their Relevance in Conservation and Sustainable Agro-Ecosystem. In: Rustagi A, Chaudhry B (Eds) Plant Reproductive Ecology. IntechOpen, Rijeka. https://doi.org/10.5772/intechopen.100531

Núñez González N, Boado M, González L, Rodríguez J (2023) Do plant-herbivore interactions recover after the invasive plant *Carpobrotus* spp. is removed? Book of abstracts. https://iyrcis.webs.uvigo.es/assets/files/Book-ofAbstractsIyrCIS2023.pdf

Ollivier M, Lesieur V, Raghu S, Martin J-F (2020) Characterizing ecological interaction networks to support risk assessment in classical biological control of weeds. Current Opinion in Insect Science 38: 40–47. https://doi.org/10.1016/j.cois.2019.12.002

Ollerton J (2017) Pollinator diversity: distribution, ecological function, and conservation. Annual review of ecology, evolution, and systematics 48(1): 353–376. https://doi.org/10.1146/annurev-ecolsys-110316-022919

Oksanen J, Blanchet FG, Friendly M (2020) Vegan: Community Ecology Package (Version 2.5–5). https://cran.r-project.org/web/packages/vegan/index.html

Parra-Tabla V, Arceo-Gómez G (2021) Impacts of plant invasions in native plant–pollinator networks. The New Phytologist 230: 2117–2128. https://doi.org/10.1111/nph.17339

Portela R, Barreiro R, Alpert P, Xu C-Y, Webber BL, Roiloa SR (2023) Comparative invasion ecology of Carpobrotus from four continents: Responses to nutrients and competition. Journal of Plant Ecology 16(1): rtac034. https://doi.org/10.1093/jpe/rtac034

Pyšek P, Richardson DM (2010) Invasive Species, Environmental Change and Management, and Health. Annual Review of Environment and Resources 35: 25–55. https://doi.org/10.1146/annurev-environ-033009-095548

R Core Team (2022) R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/

Rodríguez J, Cordero-Rivera A, González L (2021) Impacts of the invasive plant *Carpobrotus edulis* on herbivore communities on the Iberian Peninsula. Biological Invasions 23: 1425–1441. https://doi.org/10.1007/s10530-020-02449-5

Roiloa SR (2019) Clonal traits and plant invasiveness: The case of Carpobrotus N.E.Br. (Aizoaceae). Perspectives in Plant Ecology, Evolution and Systematics 40: 125479. https://doi.org/10.1016/j.ppees.2019.125479

Sakagami SF, Fukuda H (1973) Wild Bee Survey at the Campus of Hokkaido University (With 20 Text-figures and 9 Tables). Journal of the Faculty of Science Hokkaido University Series VI. Zoology : Analysis of Complex Systems, ZACS 19: 190–250. http://hdl.handle.net/2115/27559

Silveira F, Melo G, Almeida E (2002) Abelhas Brasileiras: Sistemática e Identificação. Published by the authors, Belo Horizonte, 1–253.

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions 1: 21–32. https://doi.org/10.1023/A:1010086329619

Valido A, Rodríguez-Rodríguez MC, Jordano P (2019) Honeybees disrupt the structure and functionality of plant-pollinator networks. Scientific Reports 9: 4711. https://doi.org/10.1038/s41598-019-41271-5

Vanbergen AJ, Insect Pollinators Initiative (2013) Threats to an ecosystem service: pressures on pollinators. Frontiers in Ecology and the Environment 11(5): 251–259. https://doi.org/10.1890/120126

Vázquez DP, Melián CJ, Williams NM, Blüthgen N, Krasnov BR, Poulin R (2007) Species abundance and asymmetric interaction strength in ecological networks. Oikos 116(7):1120–1127. https://doi.org/10.1111/j.0030-1299.2007.15828.x

Weiskopf SR, Rubenstein MA, Crozier LG, Gaichas S, Griffis R, Halofsky JE, Hyde KJW, Morelli TL, Morisette JT, Muñoz RC, Pershing AJ, Peterson DL, Poudel R, Staudinger MD, Sutton-Grier AE, Thompson L, Vose J, Weltzin JF, Whyte KP (2020) Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. The Science of the Total Environment 733: 137782. https://doi.org/10.1016/j.scitotenv.2020.137782

Appendix 1

Table A1. Bee species per network in the Dunas da Lagoa da Conceição Natural Municipal Park, southern Brazil.

Bee species	Network			
	I	U1	M	U2
Apis mellifera	X	X	X	X
Augochlora sp.	X	X	–	X
Augochlorella michaelis	–	X	–	–
Augochlorella sp.	X	X	X	X
Augochloropsis sp.	–	–	X	X
Bombus morio	–	X	–	–
Callonychium sp.	X	X	X	X
Centris sp.	–	X	X	–
Ceratina (*Ceratinula*) sp.	X	–	X	X
Ceratina (*Crewella*) sp.	X	–	X	X
Ceratina sp.	X	–	X	–
Colletes sp.	–	–	X	X
Epicharis sp.	–	X	X	–
Eufriesea smaragdina	–	X	X	X
Hexantheda sp.	X	X	X	X
Lasioglossum (*dialictus*) sp.	X	X	X	X
Megachile (*Austromegachile*) *susurrans*	–	–	–	X
Megachile (*Leptorachis*) sp.	X	X	–	X
Megachile (*Moureapis*) sp.	X	X	–	–
Megachile (*Pseudocentron*) sp.	X	X	–	X
Megachile sp.	X	–	–	–
Melipona quadrifasciata	X	X	X	X
Melitoma segmentaria	X	–	X	–
Mesonychium littoreum	X	X	X	X
Pseudagapostemon (*Pseudagaspotemon*) *brasiliensis*	X	X	X	X
Tetrapedia sp.	X	–	–	–
Thectochlora hamate	X	X	–	X
Trigona spinipes	X	–	X	–
Xylocopa brasilianorum	X	X	X	X

(X) indicates the presence of the species, while (–) indicates the absence of the species in the network. Networks represented as follows: Invaded (I); Uninvaded first year (U1); Managed (M); Uninvaded second year (U2). Source: Serigheli, L. F. C.

Table A2. Flowering plant species per network in the Dunas da Lagoa da Conceição Natural Municipal Park, southern Brazil.

Plant species	Network			
	I	U1	M	U2
Acicarpha spathulata	X	X	X	X
Aechmea sp.	–	X	–	–
Alternanthera brasiliana	X	X	–	X
Asclepias mellodora	–	X	–	–
Canavalia rosea	–	X	–	X
*Carpobrotus acinaciformis**	X	–	–	–
Cordia curassavica	X	X	X	X
Crinum asiaticum	–	–	X	–
Dalbergia ecastophyllum	X	–	–	X
Diodia radula	X	X	X	X
Evolvulus pusilus	–	–	–	X
Guapira opposita	X	X	X	X
Hydrocotyle bonariensis	X	–	X	–
Ipomea imperati	X	X	–	–
Ipomea pes-caprae	X	X	X	–
Mikania involucrata	X	X	X	X
Noticastrum sp.	–	X	–	X
Oenothera mollissima	X	X	–	X
Opuntia monacantha	X	X	X	X
Oxypetalum tomentosum	–	X	–	–
Petunia littoralis	X	X	X	X
Polygala cyparissias	X	X	X	X
Porophyllum ruderale	X	X	X	X
Scaevola plumieri	–	X	X	X
Senecio sp.	X	X	X	–
Solanum sp.	–	X	–	X
Sophora tomentosa	X	X	X	X
Stylosanthes viscosa	X	X	–	X
Symphyopappus casarettoi	–	X	X	X
Vernonia sp.	X	X	X	X

(*) exotic invasive plant, (X) indicates species presence, (–) indicates species absence in the network. Networks are represented as follows: Invaded (I); Uninvaded, year 1 (U1); Managed (M); Uninvaded, year 2 (U2). Source: Serigheli, L. F. C.

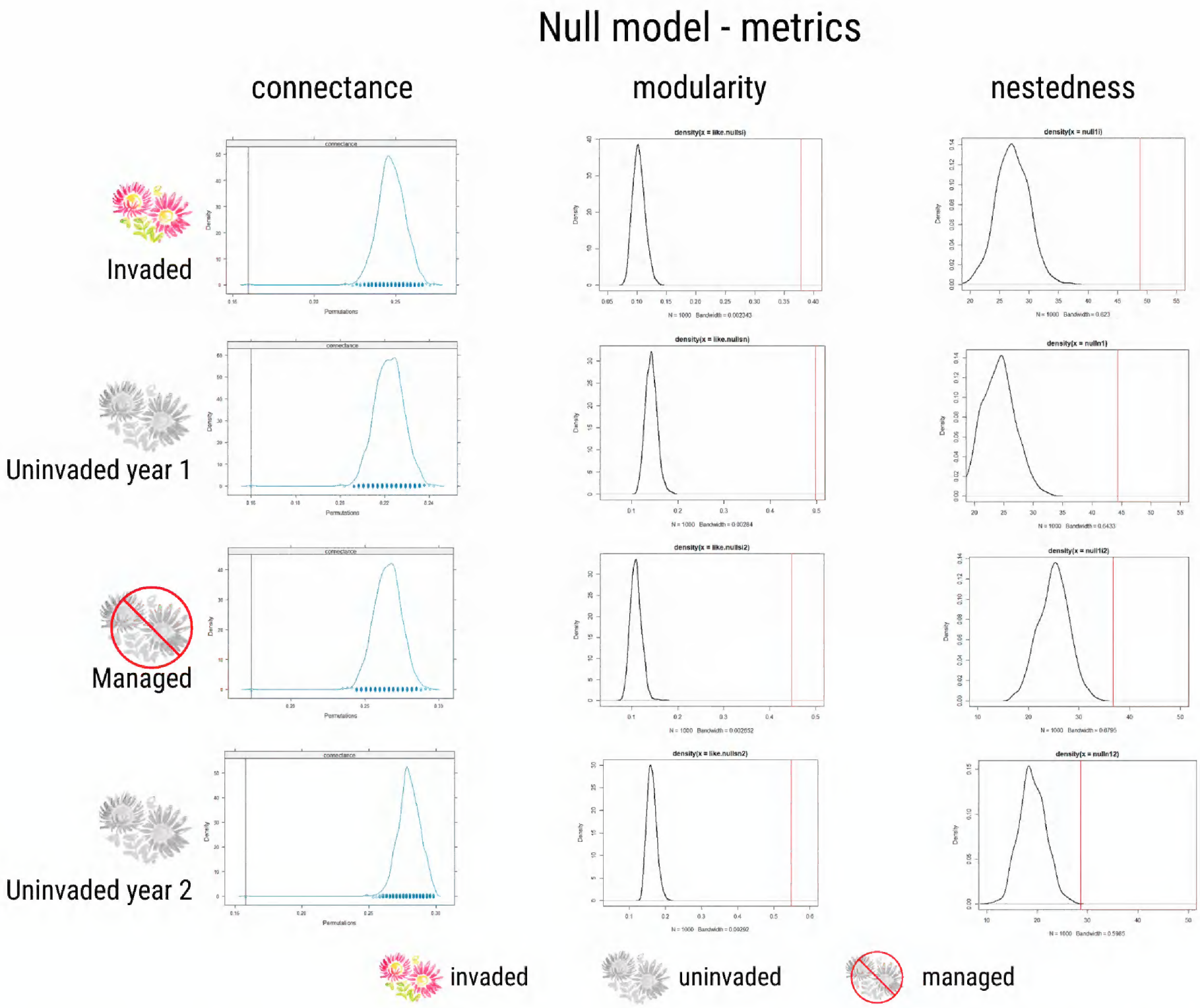

Figure A1. Null-models of all metrics for regular networks in the Dunas da Lagoa da Conceição Natural Municipal Park, southern Brazil. Invaded (I); Uninvaded year 1 (U1); Managed (M); Uninvaded year 2 (U2). Source: Serigheli, L. F. C.

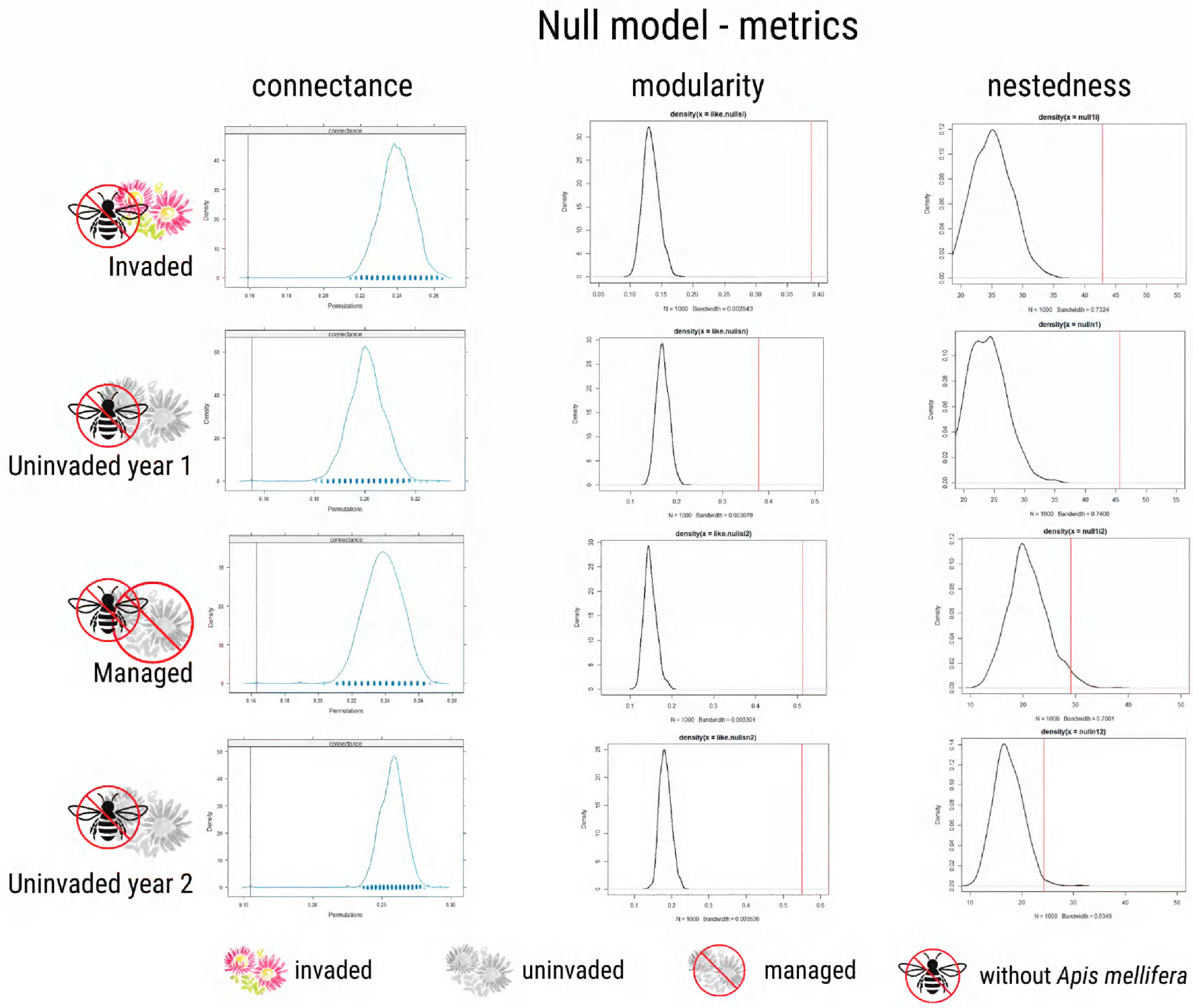

Figure A2. Null-models of all metrics for each of the following networks simulating elimination of *Apis mellifera* in the Dunas da Lagoa da Conceição Natural Municipal Park, southern Brazil. Invaded (Ia); Uninvaded year 1 (U1a); Managed (Ma); Uninvaded year 2 (U2a). Source: Serigheli, L. F. C.